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Speciation dynamics in the noctuid moth *Plusia chrysitis* L.

(Lepidoptera, Noctuidae)

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Abstract

Plusia chrysitis L. is a widespread noctuid moth in temperate Europe. A form, in which both metallic bands across the forewing are connected (= forma juncta), extends across temperate Asia to the east. The taxonomic status of this form is quite uncertain. Some authors include it into the taxon *P. chrysitis* as a (seasonal) form. Others treat it as a valid species *Plusia tutti* (Kostrowicki) despite the extraordinary high degree of variation in the genitalia. Both "forms" occur together in Central Europe, but 'juncta' is much more abundant in southeastern Bavaria than expected. Light-trap captures in the Lower Bavarian valley of the river Inn, which were made in the period from 1969 to 1982, show a clearcut seasonal separation and revealed a very low degree of intermediary forms (1.2 per cent). The form 'juncta' flies earlier in season with a first maximum in early June and a second one in early August. *P. chrysitis* attains its first peak in early July or towards the end of June and a second one in late August or early September. There is, therefore, a sufficient separation in time of season (allochronic occurrence) to keep the gene pools of both taxa separated. The form 'juncta' may represent or include at least a valid species, which was described by Kostrowicki as *Plusia tutti*. Since there is some degree of intermediary forms the hypothesis is discussed that *P. chrysitis* is a western and *P. tutti* an eastern population. The latter may be spreading towards the west.

The separation of both taxa is perhaps not complete yet. They may be still in the process of speciation.

1. Introduction

Plusia chrysitis L. is a common noctuid moth in the palearctic region. The range extends from the British Isles and the Iberian Peninsula through Central Europe and the southern parts of Northern Europe to Japan and the Far East. Within this very extensive range one would expect a number of geographically well defined populations in the taxonomic rank of subspecies. But Kostrowicki (1961) showed, that the whole complex is probably composed of two sibling species, which can be largely separated according to the metallic bands on the forewings. The nominate form is *Plusia chrysitis* L.. The metallic bands are well separated and mostly without a connection in between (fig. 1). The other species *Plusia tutti* (Kostrowicki) shows a broad connection of both metallic bands, and this type has been called forma juncta. This taxon predominates in Eastern Europe. In the Asian part of the range it is the single form existing. But in the west it is replaced by the other species *Plusia chrysitis*. The conclusion of Kostrowicki (1961) was based on differences in the genitalia, which coincided to some degree (but not completely) with the presence or absence of the connection between the metallic bands.

Lempke (1965) examined specimens from Dutch collections. At first he agreed with Kostrowicki (1961), but in a second paper (Lempke 1966) he doubted whether the morphological features are conclusive enough to keep both species valid. There was too much variation in the form of the valves, a result which is quite surprising, because the structure of the genitalia normally is specific enough to separate very similar moth species. This amount of variation led Lempke (1966) to the conclusion, that the two

taxa are simply forms of one species, a view which was strenghtened by the results of KRISTENSEN (1966), who assumed that both 'species' are simply seasonal morphs of *P. chrysitis*. So the problem seemed to be settled after all.

But some questions remained unsolved, e. g. the pronounced cline of relative abundance of both forms from the west to the east. Or the fact that one could find easily some intermediary specimens and that both forms could be found flying at any season.

Quantitative field date were lacking obviously, because all the conclusions were drawn from museum material. The aspects of population genetics had not been investigated which would be essential in the understanding of a seasonal dimorphism (cf. FORD 1964). The species concept too was not convincing, which had been applied by LEMPKE (1966) and KRISTENSEN (1966), because they were not able to look at frequencies of the two morphs within natural populations (MAYR 1963). New data providing information on that aspects would be desirable, therefore, for a new look at this problem.

2. Material and methods

A total of 1583 specimens of both forms had been collected by means of light-trap captures in the Southeastern Bavarian valley of the river Inn. One trap was operated on the outskirts of the village of Aigen (48.18 N 13.16 E) and another one in the riverine woodland along the Inn river. Gardens and meadows, fields and open woodland (deciduous) surround the trap positions. The light-traps use ultraviolet-rich "blue" light, and the moths are captured alive. After checking they could fly away next morning. A total of 378 nights could be evaluated for this study.

The grand total of both traps showed no significant differences in the frequency of the juncta-form (75 and 79 per cent respectively). The trapping results, therefore, were put together to one sample for each year. The traps are about 5 kilometres apart.

For the analysis of seasonal distribution of the capture frequencies half-month time units were used. The specimens were grouped according to the presence or absence of the connection between the golden metallic bands on the forewings. A third category contained "intermediary" specimens (fig. 1). No measures of wing length and width were taken, because the results of LEMPKE (1966) questioned their usefulness.

Trapping nights were distributed quite evenly across the total flight period of both forms (table 1). The influence of the distribution of sampling inadequacies should be low, and hence without significant effects.

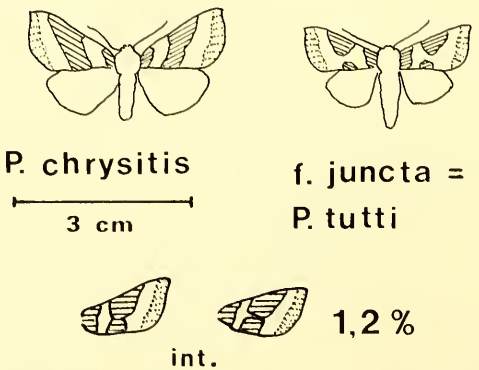

Fig. 1: Typical wing pattern of the two forms of *Plusia chrysitis* L.. The form 'juncta' is now considered to include a valid species *Plusia tutti* (Kostrowicki). The intermediary forms make up to 1.2 per cent in the study area.

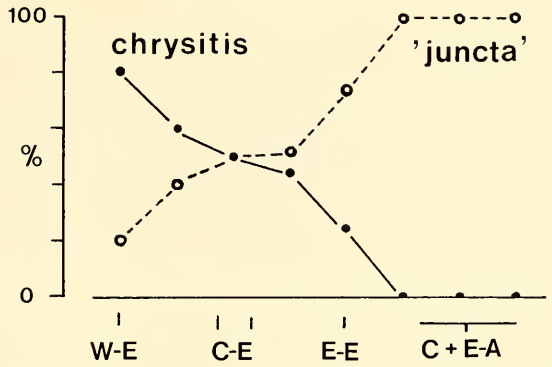

Fig. 2: Percentage of the forms of *Plusia chrysitis* L. in the clines from Western Europe (W–E), Central (C–E) and Eastern Europe (E–E) to Central and Eastern Asia (C + E–A) (redrawn from KOSTROWICKI 1961)

3. Results

3.1 Percentage of the 'forms'

According to KOSTROWICKI (1961) one could expect roughly equal numbers of both species in the study area, which is situated in Central Europe. But the form juncta reached between 57 and 90 per cent in the Lower Bavarian valley of the Inn river (cf. tab. 2). The area is 320 metres above sea level and climatically part of the transition belt between the oceanic and continental climates. The annual fluctuations may be the results of weather fluctuations. Nevertheless the composition resembles more closely the situation in the pre-Uralian areas than Central European condition, if KOSTROWICKI's (1961) results are (still) valid. Caution may be appropriate, because fig. 4 shows a tendency for the nominate form to decrease over time. This potential increase in the form juncta is not significant and perhaps of no further meaning than annual variation around the average of 80 ± 8 per cent. If the material is separated into two periods from 1969 to 1974 and 1975 to 1982 no differences in the averages can be detected (21 ± 13 and 19 ± 3 per cent respectively for the nominate form).

Table 1: Seasonal distribution of light-trap captures in the Lower Bavarian valley of the Inn river for the years 1969 to 1977

month	May	June	July	August	September
number of trapping nights	102	78	73	70	55

Table 2: Annual percentage of the nominate form *Plusia chrysitis* in the light-trap captures

Year	1969	1971	1972	1973	1974	1975	1976
N (total)	153	101	78	122	140	62	90
% nom.	23	18	10	43	14	22	17
Year	1977	1978	1979	1980	1981	1982	
N (total)	93	167	118	134	198	127	
% nom.	15	22	22	19	21	16	

Ø = 20 ± 8 % total sum of specimens 1583

3.2 Seasonal differences

The pattern of seasonal flight activity of both forms is shown in fig. 3. The juncta-form preceds the nominate form by more than half a month in both flight periods, which are well separated. The degree of overlap attains a value of only 21 per cent in this type of graphical presentation. In reality it is still lower, because in many nights of the overlapping periods each year only one form is flying. The small changes in flight time and flight conditions from year to year generate some apparent overlap. The real overlap is lower than 10 per cent in fact. The average falls as low as 4.2 per cent, and in some years it is zero.

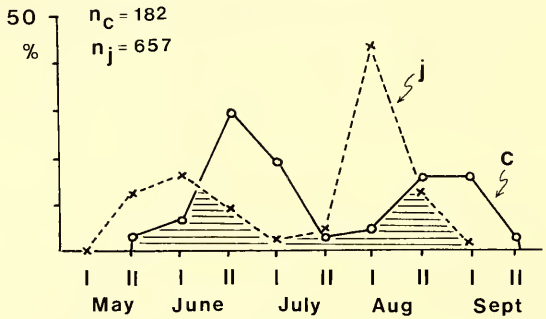

Fig. 3: Seasonal segregation of the nominate form *chrysitis* (c) and the 'juncta' form (j) in the East Bavarian light trap captures (abscissa = half month units). Shaded area = time zone with complete overlap.

3.3 Frequency of intermediate specimens

True intermediate specimens were found quite rarely. They amount to 1.2 per cent in the whole material of 744 specimens, which had been checked thoroughly enough. Two of them had a small fusion on one, but none on the other wing.

3.4 Frequency in the city of Munich

In the years of 1981 to 1984 light-trap captures similar to those in Lower Bavaria were made in an enclosed courtyard in Nymphenburg castle in Munich at the State Zoological Museum. 8 juncta and 9 nominate forms were captured, thus indicating the 50:50 level expected for Central Europe. But the size of the sample is too small to be conclusive.

4. Discussion

The results of the light-trap captures may be summarized in the following statements:

- the average percentage of the juncta form in the Lower Bavarian Inn valley is much higher than expected (80%)
- the amount of seasonal separation of the two forms is sufficient to interrupt a free genetic exchange
- the very low incidence of intermediate forms (1.2%) strongly indicate the allochronous separation of the two forms.

Without further morphological considerations these findings would be compatible with a separation into two seasonally different species, as Kostrowicki (1961) had done it. Such a view would be consistent with modern species concepts (Mayr 1963). But nevertheless the high variability in the genitalia

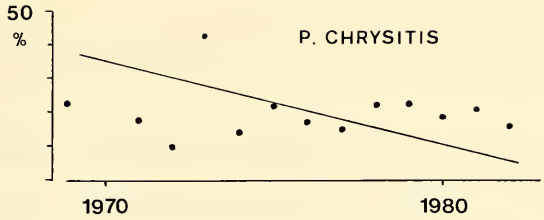

Fig. 4: Development of the percentage of *Plusia chrysitis* in the total catch per year from 1969 to 1982.

found by other researchers is puzzling. The occurrence of intermediary specimens, though very low in frequency, may likewise argue against a "good" separation into two species. How can this puzzle be solved?

One important factor, perhaps, is the distribution of both forms across the area of occurrence. They follow a cline (cf. fig. 2) with two ends of pure forms in the east and in the west. They overlap in Central Europe in a broad area. The results from Lower Bavaria indicate, perhaps, a shifting of the frequencies in the last two decades, at least locally, towards juncta. *Plusia chrysitis* on the other hand, may be an Atlantic "version", which predominates in the regions with oceanic climate because of its later flying dates, whereas *Plusia tutti* represents the continental adaptive type, which dominates even in quite western areas, like the Lower Bavarian Inn river valley, which are climatically transitional. The earlier flying date provides a means of avoiding *P. chrysitis* and/or outcompeting it in the continental areas. Since the amount of time overlap is so small (less than 10 per cent), the separation of both species in time is sufficient to keep the gene pools apart despite high similarities (and variation) in the genitalia.

Central Europe provides a transitional belt for quite a number of sibling species or subspecies, e. g. the famous examples of the Carrion and Hooded Crow *(Corvus corone corone* and *C. corone cornix)* with a very small contagious zone along the river Elbe (Mayr 1963). Both taxa remain at the subspecific level, but in biological terms they may be viewed as semi-species with a markedly decreased fitness of

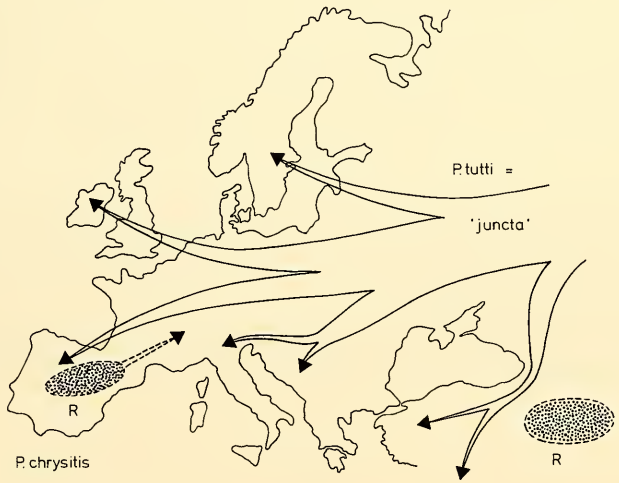

Fig. 5: Possible scenario for the spreading of the form 'juncta', i. e. *Plusia tutti,* in the postglacial period and the invasion of the areas of *P. chrysitis,* which survived in at least two refugia (R) in the Iberian peninsula and perhaps in southwestern Asia.

their hybrids. On the other hand subspecies of the Long-tailed Tit *(Aegithalos caudatus)* meet in a broad hybridization belt in Central Europe. The stripe-headed and white-headed forms from the west and from the east invade each other genetically without recognizeable reduction in fitness across some 1 000 kms width.

Taxonomic decision must be, therefore, somewhat arbitrarily in such cases. But with respect to the results of the seasonal separation and the low incidence of "hybrids" the rank of a species should be given to *Plusia tutti* sensu KOSTROWICKI (1961). This is considered to be taxonomically appropriate.

As indicated above, the pattern of occurrence of both species can be used to construct a hypothesis concerning the evolution of both taxa (cf. fig. 5). *Plusia tutti* should have survived the pleistocene period in an eastern refugium, from which it spread to the west with the improvement of climatic conditions. *Plusia chrysitis* on the other side could have survived in the oceanic refugia in the southwest of Europe, but being adapted to such weather conditions prevailing in the oceanic climate influenced regions, its capability of expansion towards the east was impeded by climatic factors. This could have given the superiority of *P. tutti* with respect of size of area and its movement towards the west into the area of *P. chrysitis*. The small amount of intermediate forms shows, that both species are probably still in the process of speciation – in statu nascendi*.

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Zusammenfassung

Dynamik der Artbildung bei der Messingeule *Plusia chrysitis* L. (Lepidoptera, Noctuidae)

Die Messingeule *Plusia chrysitis* L. kommt im gemäßigten Klimabereich Europas weit verbreitet vor. Eine Form, bei der die beiden golden-metallisch glänzenden Bänder auf den Vorderflügeln durch einen deutlichen Steg miteinander verbunden sind, wird als forma juncta bezeichnet. Ihr Areal erstreckt sich von Mitteleuropa bis Ostasien und Japan. Einige Autoren behandeln diese Form als eigene Art *Plusia tutti* (Kostrowicki), obwohl die Zuordnung wegen erheblicher Variabilität der Genitalapparatur Schwierigkeiten bereitet. Juncta ist im Südostbayerischen Inntal mit rund 80% Anteil an den Lichtfallen-Fängen beider Formen erheblich häufiger, als nach dem Trend von West nach Ost zu erwarten wäre. Das Untersuchungsgebiet zählt allerdings klimatisch bereits zum kontinentalen Übergangsbereich.

Die Lichtfallenfänge mit Lebendfang-UV-Fallen zeigten zudem, daß sich die Flugzeit beider Formen in charakteristischer Weise voneinander unterscheidet. Juncta (incl. *tutti)* fliegt um gut einen halben Monat in der ersten wie auch in der zweiten Flugperiode früher als *P. chrysitis.* Die Maxima liegen Anfang Juni und Anfang August bei *P. tutti* und Ende Juni bzw. Mitte September bei *P. chrysitis.* Intermediäre Formen treten überraschend selten (1.2%) auf, wenn man beide Formen als Angehörige der gleichen Art betrachtet, aber zu häufig, wenn es sich um zwei völlig getrennte Arten handeln sollte.

Die Befunde deuten auch darauf hin, daß sich *f. juncta* nach Westen ausbreitet und daß sie von *P. chrysitis* noch nicht vollständig genetisch isoliert ist – also gleichsam ein Artenpaar in statu nascendi darstellt.

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* Most results of this publication have been presented on the occasion of the 49. Meeting of Entomologists in Linz/Austria in a lecture entitled „Die Form juncta der Messingeule *Plusia chrysitis* (L.) – eine Art in statu nascendi?", Nov. 7th, 1982.

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Postscript

After completion of this study the author received some information about similar results concering the species status and its validity of *Plusia tutti*, which were drawn from studies on the pheromone discrimination in both species. These results are to be published quite simultaneously in Mitt. schweiz. Ent. Ges. by E. PRIESNER (Max-Planck-Institut für Verhaltensphysiologie, Seewiesen). I would like to express my kind thanks for this cooperation. PRIESNERs studies broaden the scope and improve greatly the validity of the taxonomic statement on *P. tutti*.

According to the results on pheromone attraction the form juncta also includes some specimens, which have to be included to *P. chrysitis*. So there is no simple equality between the different forms and the different species, which makes it also difficult to interpret intermediary forms as hybrids. The pheromone studies will be more decisive. They shall be extended in the 1985 season to the study area in Southeastern Bavaria.

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